Received: 3 October 2020 | Accepted: 8 February 2021

DOI: 10.1002/csc2.20485

Crop Science

ORIGINAL RESEARCH ARTICLE

Crop Breeding & Genetics

Identifying quantitative trait loci for lodging-associated traits in the wheat doubled-haploid population Avalon × Cadenza

Francisco J. Piñera-Chavez[1] | **Peter M. Berry**[3] | **Michael J. Foulkes**[2] | **Sivakumar Sukumaran**[1] | **Matthew P. Reynolds**[1]

[1] Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico 56237, Mexico

[2] Division of Plant and Crop Sciences, The Univ. of Nottingham, Sutton Bonington Campus, Loughborough, Leicestershire LE125RD, UK

[3] ADAS High Mowthorpe, Malton, North Yorkshire YO178BP, UK

Correspondence
Francisco J. Piñera-Chavez, Global Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Texcoco, Mexico, 56237, Mexico.
Email: f.pinera@cgiar.org

Assigned to Associate Editor Eric Olson.

Abstract

Lodging affects grain quality and grain yield in wheat (*Triticum aestivum* L.) and is difficult to breed for because its sporadic incidence and laborious protocols to measure lodging traits. Thus, developing molecular markers for these traits can increase selection efficiency in breeding programs. The aim of this article is to identify quantitative trait loci (QTL) associated with stem/anchorage strength and leverage traits (lodging traits) in a doubled-haploid population of UK bread wheat Avalon × Cadenza. Field experiments were conducted in the UK during 2012–2013 near High Mowthorpe and during 2013–2014 at Sutton Bonington. Phenotypic and genetic analysis indicated significant genetic variation for all traits. Stem strength (diameter, wall width, and material strength) and leverage (plant height) traits were highly heritable (0.64–0.95), whereas anchorage strength traits (root plate spread and structural rooting depth) and ear number per plant (leverage trait) were less heritable (0.21–0.33). This study identified 18 QTL for lodging traits and grain yield in chromosomes 1D, 2B, 2D, 3A, 3B, 4A, 4D, 5B, and 6B. Two QTL for stem strength on chromosome 1D and 3B explaining 49.6% of the total phenotypic variation (PVE) are estimated to reduce stem lodging risk and shortening the plant height by 12 cm. One QTL for root plate spread on chromosome 5B explaining 22.4% of the PVE could increase root lodging resistance.

1 | INTRODUCTION

The Green Revolution in the 1960s and 1970s that produced the semi-dwarf cultivars (Conway, 1997) reduced the leverage on the stem base and anchorage system in wheat (*Triticum aestivum* L.) plants, thereby increasing the lodging resistance (Berry et al., 2004). Since then wheat yields have increased in breeding programs worldwide (Crespo-Herrera et al., 2017; Fischer et al., 2014; Foulkes et al., 2009; Gerard et al., 2020; Lopes et al., 2012; Tadesse et al., 2019), either with no further change in plant height (Berry et al., 2015) or with increased plant height (Aisawi et al., 2015), and this has contributed to increased shoot and plant leverage. Therefore, reducing

Abbreviations: DArTs, diversity arrays technology; DEFRA, Department of Environment, Food and Rural Affairs; DH, doubled-haploid; ENPP, ear number per plant; GS, genomic selection; GY, grain yield; H^2, broad sense heritability; HM, High Mowthorpe; IBS, internode breaking strength; ID, internode diameter; IL, internode length; IMS, internode material strength; IWW, internode wall width; LOD, logarithm of odds; LTM, long-term mean; MAS, marker assisted selection; NABIM, National Association of British and Irish Millers; PH, plant height; PVE, phenotypic variation explained; QTL, quantitative trait loci; REML, restricted maximum likelihood; RPS, root plate spread; SB, Sutton Bonington; SED, standard error of difference; SNPs, single nucleotide polymorphisms; SSRs, simple sequence repeats; SRD, structural rooting depth; WGIN, Wheat Genetic Improvement Network.

lodging in wheat remains an important strategy to maintain high yields and grain quality, especially in high-yielding environments.

For instance, in the UK, no significant trend was observed on the reduction of plant height of winter wheat after the 1990s (Berry et al., 2015), whereas the plant height of spring wheat developed by CIMMYT breeding programs has increased in recent decades (Aisawi et al., 2015). Thus, novel ways to counteract this increased shoot and plant leverage will be needed. The most recent detailed lodging literature review by Berry et al. (2004) has indicated that to counteract these forces it is necessary to strengthen the stem base and anchorage system. This can be done by exploiting the biophysical properties of these components of the plant (lodging-related traits), which include root plate spread, structural rooting depth, and anchorage strength of the root system and diameter, wall width, breaking strength, length, stem strength, and material strength of the stem base. Berry et al. (2007) reduced the number of traits to a set of key traits. These included the root plate spread (main determinant of anchorage strength), diameter, material strength, and wall width of the stem base (determinants of stem strength) and plant height (main determinant of shoot and plant leverage). Genetic variation of lodging-related traits was found for winter wheat crops grown in the UK (Berry et al., 2003b, 2007; Berry & Berry, 2015) and for spring wheat grown in northwest (NW) Mexico (Piñera-Chavez et al., 2016b). Additionally, several other studies have indicated genetic variation for lodging traits in winter and spring wheat (Hai et al., 2005; Kelbert et al., 2004; Keller et al., 1999; Tripathi et al., 2003; Verma et al., 2004; Wiersma et al., 2011). Berry et al. (2007) and (Piñera-Chavez et al., 2016a), respectively, estimated the dimensions of a lodging-proof wheat crop for the UK (winter wheat) and NW Mexico (spring wheat) growing conditions. Achieving this lodging-proof crop will depend on the interrelationships of lodging-related traits and optimizing the combination of key trait targets in a single variety. No studies have reported any strong genetic linkages between traits that could prevent the lodging-proof ideotype from being achieved (Berry & Berry, 2015; Piñera-Chavez et al., 2016b). However, strong genetic linkage between stem strength and stem wall width will increase the biomass cost about 22% (if maximum stem wall width observed value is considered) for stronger stems in spring wheat (Piñera-Chavez et al., 2016b). This will potentially represent a trade-off between stem strength and yield-formation processes (e.g., accumulation of stem soluble carbohydrate reserves). Another key limitation will be that current genetic ranges for root plate spread are not sufficient to achieve the ideotype target (Piñera-Chavez et al., 2016b) and may compromise breeding for root-lodging resistance. Thus, there is a requirement to find variation for this trait in more diverse germplasm to deploy in root plate spread breeding among elite materials.

Core Ideas

- Sixteen quantitative trait loci identified for lodging resistance traits.
- Specific region in chromosome 3B related to overall stem strength.
- Specific region in chromosome 5B related to root plate spread.

The amount of time required to assess lodging traits will constrain the capacity of selection for lodging resistance in wheat. Optimizing the number of traits and plant sample size (Piñera-Chavez et al., 2020), together with automation of lodging devices for direct measurements in the field (Berry et al., 2003a; Niu et al., 2012), can increase this selection capacity. Despite the reduction of time for lodging assessment conferred by these approaches, the use of reliable molecular markers perhaps represents the most efficient long-term strategy to advance lodging resistance together with increases in yield.

Molecular markers in wheat are currently being implemented by modern breeding strategies or molecular breeding where the use of genetic markers is complementing phenotypic selection to accelerate development and delivery of improved cultivars (Ribaut et al., 2010). However, to develop these genetic markers it is necessary to carry out phenotypic screening and genetic mapping of wheat in order to identify quantitative trait loci (QTL) that can be further developed into reliable genetic markers. According to Berry and Berry (2015), the genetic control of lodging-related traits, particularly, those associated with stem and anchorage strength has not been fully understood, in fact, investigations were mostly done on a limited range of germplasm and seasons and some key traits such as root plate spread were not measured in field-grown crops. These authors reported a comprehensive genetic analysis of traits related to lodging in two winter wheat doubled-haploid mapping populations; however, whether the QTL identified are consistent or not in other genetic backgrounds was not demonstrated.

Identifying QTL related to lodging resistance traits represents a promising aspect to accelerate selection for lodging resistance in wheat. Recently, QTL linked to stem diameter (Berry & Berry, 2015; Hai et al., 2005; Keller et al., 1999), stem wall width (Berry, & Berry, 2015; Hai et al., 2005), stem strength, stem material strength, root plate spread, and root plate depth (Berry, & Berry, 2015) have been identified. Gene *TaCM*, involved in the biosynthesis of lignin, was also associated to the stem strength (Ma, 2009). Some studies identified some associations of lodging-traits with grain yield that will need further investigation (e.g., with plant height, stem wall width, and material strength). Possible trade-offs

between stem strength traits and grain yield can be minimized if QTL linked to both yield and straw biomass (Berry et al., 2008; Li et al., 2014) can be exploited.

The aim of this study was to understand the genetic basis of the key lodging traits that determine stem and anchorage strength and plant leverage through QTL mapping. This will help to develop genetic markers and enable breeders to rapidly screen for these traits, which are laborious to measure but vital for counteracting increased lodging resistance brought about by increases in yield and in some cases greater plant height.

2 | MATERIALS AND METHODS

2.1 | Field experiments and plant material

Plant material used in this study consisted of a subset of 84 wheat lines from a doubled-haploid (DH) population derived from an F_1 progeny of a cross Avalon × Cadenza. This subset represented the genetic background of a full set 203 lines that the Avalon × Cadenza DH mapping population comprised. The whole population was developed by Clare Ellerbrook, Liz Sayers, and the late Tony Worland (John Innes Centre), as part of a Defra funded project led by ADAS. The parents were originally chosen (to contrast for canopy architecture traits) by Steve Parker (Central Science Laboratory, York, UK), Tony Worland, and Darren Lovell (Rothamsted Research). Avalon is a UK semi-dwarf winter wheat released in 1979 (National Association of British and Irish Millers [NABIM] Group 1, bread making wheat) (crop height = 65.6 cm; Bai et al., 2013), and Cadenza, a UK tall spring wheat with high ratio of wall thickness to stem diameter released in 1991 (NABIM Group 2, bread making wheat) (crop height = 75.1 cm; Bai et al., 2013). The contrasting canopy architecture traits in the parents included plant height, leaf size, and angle (Snape et al., 2007). Avalon × Cadenza DH mapping population is considered as the UK reference population under the UK Department of Environment, Food and Rural Affairs (DEFRA), and Wheat Genetic Improvement Network (WGIN).

Field experiments were conducted during 2012–2013 near ADAS High Mowthorpe, North Yorkshire (54.1° N, 0.5° W) and during 2013–2014 at Sutton Bonington, University of Nottingham farm (52.8° N, 1.24° W) (henceforth referred as High Mowthorpe and Sutton Bonington, respectively). The soil types were both sandy loams. The DH lines were arranged in a resolvable incomplete block design (Alpha Lattice Design). The High Mowthorpe experiment consisted of each DH line replicated three times in plots measuring 6 by 2 m, each replicate contained 12 blocks and each block contained seven DH lines. At Sutton Bonington, each treatment was replicated three times in plots measuring 6 by 1.65 m, each replicate contained 8 blocks and each block contained 11 DH lines. The experiments were sown on 21 Oct. in 2012 at High Mowthorpe and 8 Oct. in 2013 at Sutton Bonington. The seed rate was standardized according to thousand grain weight and was 250 and 350 seeds m^{-2} for High Mowthorpe and Sutton Bonington, respectively. Nitrogen fertilizer was provided in both experiments in amounts of 190 kg ha^{-1} for High Mowthorpe and 180 kg ha^{-1} for Sutton Bonington as ammonium nitrate prill (34.5% N). Preventive controls of diseases, weeds, and pests were applied when necessary to assure optimum conditions for crop growth and development. Plant growth regulators were not used in High Mowthorpe and two applications were done at Sutton Bonington.

2.2 | Weather conditions

Long-term mean (LTM) and seasonal means (2012–2013, High Mowthorpe; 2013–2014, Sutton Bonington) for average temperature and rainfall were obtained from weather stations at or near to the experiment sites (historic data obtained from http://www.metoffice.gov.uk). The weather station used for High Mowthorpe experiment was located at ADAS High Mowthorpe (within 10 km from the field trial). On average, the Sutton Bonington experiment occurred under warmer conditions with more precipitation compared with the High Mowthorpe experiment. High Mowthorpe had colder conditions between autumn and spring (September–May) than average (LTM), specifically at the end of winter and beginning of spring, whereas summer was warmer than the LTM at this site. On the other hand, Sutton Bonington had warmer conditions than average, except for November in autumn and August in summer. Seasonal rainfall pattern was the weather parameter least consistent with the LTM in both sites. At High Mowthorpe seasonal rainfall was far below the average, except for May at the end of spring, which was considerably higher. At Sutton Bonington, the average seasonal rainfall was slightly above the long-term mean; however, there were dryer months such as November in autumn, December in winter, March and April in spring, and June and July in summer (Figure 1).

2.3 | Measurements and calculations

Measurements of the plant characters associated with lodging were done after flowering and during early grain filling (GS65–GS79) (Zadoks et al., 1974). Seven plants were sampled randomly (minimum number of plants per plot to demonstrate repeatable expression of lodging-related characters according to (Piñera-Chavez et al., 2020)), avoiding any border effect of the plot, and excavated with a hand fork to recover roots to a depth of 100 mm (crown roots). Measurements associated with lodging resistance included the root

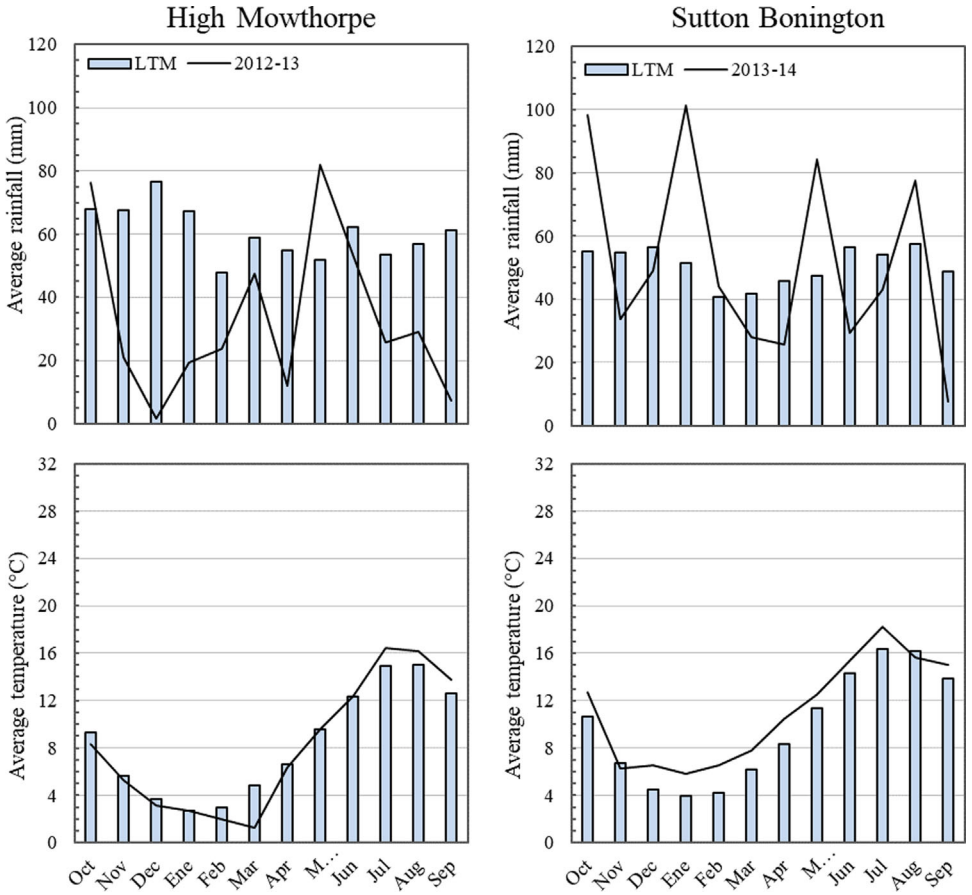

FIGURE 1 Rainfall and average temperature for High Mowthorpe (2012–2013) and Sutton Bonington (2013–2014). Long-term mean (LTM) for High Mowthorpe from 1971 to 2000 and for Sutton Bonington from 1962–2014

plate spread (RPS) and structural rooting depth (SRD) of the plant root system. Fertile ear number per plant (ENPP) and height to ear tip (plant height, PH) of the main shoot. Internode 1 of the main shoot was identified, defined as the first internode of more than 10 mm, originating at or just below the ground surface and without crown roots emerging from its upper node. Subsequent internodes ascending the shoot were numbered 2, 3, 4, etc., with the uppermost internode referred to as the peduncle. After identifying the bottom internode, the diameter (ID), length (IL), wall width (IWW), and breaking strength (IBS) of Internode 2 were measured. The detailed methods for these measurements were described in Berry et al. (2000) and the updated methodology described by (Piñera-Chavez et al., 2020) (Supplemental Table S1).

Calculations included the stem failure moment; the force required to bend a stem (N mm) (referred in the rest of the manuscript as stem strength [SS] and was calculated from the breaking strength [IBS] and length [IL] of Internode 2 (Equation 1)

$$SS = \frac{1}{4} IBS \times IL \quad (1)$$

Stem material strength (IMS) (MPa) was calculated from stem wall width (IWW), the stem diameter (ID), and stem strength (SS) of Internode 2 (Equation 2).

$$SS = \frac{IMS \times \pi \times \frac{1}{2}ID^3}{4} \times \left[1 - \left(\frac{\frac{1}{2}ID - IWW}{\frac{1}{2}ID}\right)\right]^4 \quad (2)$$

All plots were harvested with a combine harvester to measure grain yield (t ha^{-1}) (GY) in both High Mowthorpe and Sutton Bonington experiments and moisture content recorded on a grain subsample and yield adjusted to 100% DM.

2.4 | Statistical analyses

Restricted maximum likelihood (REML) of a resolvable incomplete block design (Alpha lattice design) was performed to test for differences between the treatments for each parameter for both individual and combined experiment data, considering genotype as fixed effect while replicates, sub-blocks, environment, and genotype × environment interaction (G × E) were the random effects. Adjusted means were calculated

for each trait by experiment and by combining data from both experiments. Average standard error of difference (SED) between cultivar means was calculated for individual experiments. Broad sense heritability (H^2) was calculated from variance components (Equation 4) from a mixed model performed for a combined data from both experiments were genotype, replicates, sub-blocks, environment, and genotype × environment interaction (G × E) were considered as random effects.

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + (\sigma_{ge}^2/l) + \sigma_e^2/(l \times rep)} \quad (4)$$

Equation 4 components were σ_g^2, σ_{ge}^2, and σ_e^2 where the genotype, genotype × environment interaction, and error variance components, respectively, and *rep* and *l* number of replications and number of locations, respectively. Phenotypic correlations (r_p) between traits were calculated by simple Pearson correlations. All the analyses mentioned were performed using SAS software version 9.1 (SAS Institute Inc., 2004).

2.5 | Linkage map and QTL analysis

Genetic linkage map of the full Avalon × Cadenza described before by Ma et al. (2015) and available at http:www.cerealsdb.uk.net consisted of 4,021 markers already grouped in 26 linkage groups. Each linkage group was mapped separately in Joinmap v4.1 (Van Ooijen, 2011), eliminating any redundant markers or markers closer than 0.5 cM. A genetic linkage map with 1,484 loci, which consisted of 1,190 single nucleotide polymorphisms (SNPs), 148 simple sequence repeats (SSRs) 81 diversity arrays technology (DArTs), and 65 perfect markers, was obtained. This map covered a total of 4,686 cM with an average marker interval of 3.2 cM. Genetic linkage map together with phenotypic scores (adjusted means across experiments) for each trait were subsequently used for QTL identification using the R package *R/qtl* (Broman et al., 2003) (QTL analysis by experiment was also performed and results are included in Supplemental Tables S2 and S3). Firstly, interval mapping was implemented with the Haley-Knott regression method (Knott & Haley, 1992), followed by a 1,000 permutation test (at threshold of $\alpha = .10$ tail of the null distribution) to establish a logarithm of odds (LOD) threshold to declare significant QTL (Churchill & Doerge, 1994). Subsequently, significant main effect QTL were subjected to a multiple interval mapping framework to refine positions, estimate QTL effects, and the proportion of variance explained by the QTL and the QTL model (Knott & Haley, 1992; Sen & Churchill, 2001). The confidence interval for QTL position was projected in the respective genetic map segment where a LOD drop-off of one unit occurred (Lander & Botstein, 1989). Denomination of QTL found was composed by "q" (abbreviation of QTL), trait abbreviation and linkage group (Yang et al., 2010).

3 | RESULTS

3.1 | Genetic variation

Descriptive statistics for the traits for each experiment and variance components and broad sense heritability for cross-experiment analysis are given in Table 1. Density distribution plots indicated continuous variation of these traits with approximately normal distributions, except for internode wall width where a bimodal distribution was estimated (Figure 2). This bimodal distribution may suggest the presence of a gene with segregating effect on internode wall width. The Avalon × Cadenza DH population showed statistically significant genetic differences for all traits in each experiment. There was significant G × E variation for all traits in the combined analysis. Variance components (genetic, G × E and residual variances) across years were used to calculate broad sense heritability values, which was .95 for plant height (leverage character) and ranged from .64 to .95 for stem strength, internode material strength, internode length, internode diameter, and internode wall width (stem strength characters). Heritability for structural rooting depth and root plate spread (anchorage strength related characters) was considerably lower with values of .21 (lowest) and .33, respectively. Ear number per plant (leverage character) had a heritability of .30. These results indicate that the phenotypic variation found for root plate spread, structural rooting depth, and ear number per plant was largely caused by environmental and residual factors, but environmental effects were less important for the other target traits. Heritability value for grain yield was .46.

3.2 | Association among traits

Biplot from principal component analysis (Figure 3a) and correlation coefficients (Figure 3b) were used to illustrate the interrelationships between GY and lodging traits (SS, stem strength; IMS, internode material strength; ID, internode diameter; IWW, internode wall width; IL, internode length; RPS, root plate spread; SRD, structural rooting depth; ENPP, ear number per plant; and PH, plant height). Pearson correlation coefficients (r) illustrated in Figure 3b were used to describe correlations between traits for cross-experiment means. Stem strength was positively correlated with IWW ($r = .78$, $P < .001$) and IMS ($r = .65$, $P < .001$) and negatively correlated with ID ($r = -.32$, $P < .01$). Intern-

TABLE 1 Descriptive statistics for lodging traits and grain yield for each experiment. Variance components for combined analysis across experiments

Trait	High Mowthorpe			Sutton Bonington			Variance components			
	Mean	Range	SED	Mean	Range	SED	σ^2_g	σ^2_{ge}	σ^2_e	H^2
SS, N mm	254	165–354	21.4	173	131–248	22.1	535	392	661	.64
IMS, MPa	45.8	22.5–66.8	4.12	33.8	18.9–54.8	4.64	61.6	15.4	27.2	.83
IL, mm	84.9	65.7–109	5.39	66.3	49.1–88.7	4.07	43.4	12.6	31.8	.79
ID, mm	4.02	3.51–5.07	0.13	3.94	3.34–4.72	0.12	0.096	0.0029	0.022	.95
IWW, mm	0.94	0.66–1.30	0.068	0.86	0.60–1.26	0.060	0.031	0.0012	0.0059	.90
RPS, mm	44.5	38.7–50.8	2.98	43.2	35.8–53.2	2.90	1.58	2.16	12.9	.33
SRD, mm	36.8	32.9–41.4	1.95	42.3	38.7–47.1	1.98	0.40	1.30	5.17	.21
PH, cm	85.0	64.6–111	2.74	76.3	57.9–104	2.01	127	12.2	7.73	.95
ENPP	2.62	2.08–3.89	0.27	2.87	1.98–3.58	0.39	0.019	0.039	0.16	.30
GY, t ha^{-1}	6.61	5.40–7.82	0.30	8.16	6.60–9.89	0.71	0.11	0.12	0.43	.46

Note. SS, stem strength; IMS, internode material strength; IL, internode length; ID, internode diameter; IWW, internode wall width; RPS, root plate spread; SRD, structural rooting depth; PH, plant height; ENPP, ear number per plant; GY, grain yield. SED, standard error of differences ($P < .001$, except for SRD at Sutton Bonington, $P < .01$);σ^2_g, genetic variance ($P < .001$); σ^2_{ge}, genetic × environment variance ($P < .01$–$.001$, except for SD, $P < .05$); σ^2_e, residual variance; H^2, broad sense heritability.

ode material strength and IWW were positively associated ($r = .67$, $P < .001$) and both traits were negatively correlated with ID ($r = -.90$ and $-.53$, $P < .001$, respectively). There was a strong positive correlation between RPS and SRD ($r = .67$, $P < .001$). A positive correlation between RPS and SRD with ENPP was also found ($r = .20$, $P < .07$). Plant height was positively correlated with IL ($r = .72$, $P < .001$), while negatively correlated with IWW ($r = -.31$, $P < .01$). There were also positive correlations between GY and IL ($r = .45$, $P < .001$) and PH ($r = .61$, $P < .001$) and a negative correlation between GY and IWW ($r = -.24$, $P < .05$).

3.3 | QTL analysis

Eighteen significant QTL were identified on the Avalon × Cadenza DH population for the lodging-related traits and grain yield for cross-experiment means resulting from 2 yr of phenotyping at High Mowthorpe (HM) and Sutton Bonigton (SB). A summary of the locations, significance, phenotypic variation explained (PVE) and effects of these QTL are given in Table 2. For stem strength characters (SS, IMS, ID, IWW, IL,) nine QTL were identified and were clustered on chromosomes 1D, 2D, 3A, 3B, and 4D. Only two QTL for anchorage strength traits (RPS and SRD) were found on chromosomes 5B and 6B. For leverage characters (ENPP and PH) five QTL were identified on chromosomes 2D, 3A, 3B, 4A, and 4D. Two QTL were detected for GY on chromosomes 2B and 2D. Major findings will be described in the following sections.

3.4 | Stem strength characters

For stem strength characters the QTL models explained 49.6, 57.9, 38.0, 58.3, and 81.8% of the total PVE for SS, IMS, IL, ID, and IWW, respectively (Table 2). A major finding was the identification of a genomic region in chromosome 3B with a large effect (PVE = 36.6–77.9%) on all stem strength traits, except for IL. This region was identified between 283 cM with the closest marker being *BS00003884* for IMS (PVE = 50.3%, *qIMS3B*) and ID (PVE = 36.6%, *qSID3B*) and 284 cM with the closest maker being *wPt-4412* for SS (PVE = 42.3%, *qSS3B*) and IWW (PVE = 77.9%, *qIWW3B*) (Table 2 and Figure 4). In all cases positive additive effects were given by the Cadenza allele, except for ID, where positive additive effects came from the Avalon allele (Figure 5). A relevant finding was also the presence of a genomic region located at 162 cM in chromosome 3A (closest marker *bArc19*) with a large effect given by the Cadenza allele on IL (PVE = 38.0%, *qSIL3A*) (Table 2 and Figure 5). A genomic region located at 55.2 cM in chromosome 2D (closest marker *BS00022900*) showed a major positive effect conferred by the Avalon allele on ID (PVE = 21.7%, *qSID2D*) and minor positive effect by the Cadenza allele on IMS (PVE = 7.62%, *qIMS2D*). Two more genomic regions located at 35.0 in chromosome 1D (closest marker *cfd19*) and 80.0 of chromosome 4D (closest marker *BS00021903*) had minor positive effects on SS (PVE = 7.34%, Cadenza allele) and IWW (PVE = 3.88%, Avalon allele), respectively (Table 2). Linkage among QTL affecting internode wall width (*qIWW3B* and *qIWW4D*) and internode diameter indicated the presence of epistasis for each of these traits. On the other hand, QTL identified for stem

TABLE 2 Summary of the QTL detected for cross-experiment means for lodging traits and grain yield

Trait	Chr	QTL	Position	CI	LOD	PVE	Additive effect[a]	Flanking markers[b]
			——————cM——————			%		
SS	1D	*qSS1D*	35.0	31.0–43.0	3.08	7.34	8.49 N mm (C)	*BS00060042*–***cfd19***
	3B	*qSS3B*	284	278–287	13.2	42.3	19.1 N mm (C)	***wPt-4412*** *–cos4Gb*
IMS	2D	*qIMS2D*	55.2	49.0–61.0	3.85	7.62	2.43 MPa (C)	***BS00022900*** *–BS00035934*
	3B	*qIMS3B*	283	279–287	17.1	50.3	6.23 MPa (C)	***BS00003884*** *–wPt-4412*
IL	3A	*qIL3A*	162	142–210	8.71	38.0	4.58 mm (C)	***bArc19*** *–BS00010204*
ID	2D	*qID2D*	55.2	51.0–60.0	8.00	21.7	0.148 mm (A)	***BS00022900*** *–BS00035934*
	3B	*qID3B*	283	272–288	12.0	36.6	0.197 mm (A)	***BS00003884*** *–wPt-4412*
IWW	3B	*qIWW3B*	284	283–287	29.0	77.9	0.161 mm (C)	***wPt-4412*** *–cos4Gb*
	4D	*qIWW4D*	80.0	58.0–109	3.25	3.88	0.0366 mm (A)	***BS00021903*** *–BS99999951*
RPS	5B	*qRPS5B*	195	159–205	6.77	31.0	1.17 mm (C)	*Ex42-7B*–***BS00070507***
SRD	6B	*qSRD6B*	154	148–196	3.18	16.0	0.577 mm (C)	***wPt-4858*** *–wPt-8814*
PH	2D	*qPH2D*	36.0	25.0–52.0	10.5	21.7	5.54 cm (C)	*cos2Q*–***gwm261***
	3A	*qPH3A*	145	142–202	7.98	15.3	4.59 cm (C)	***wPt-9215*** *–BS00022612*
	3B	*qPH3B*	281	233–288	3.36	5.66	2.83 cm (A)	*BS00009671*–***BS00036547***
	4D	*qPH4D*	61	56.0–69.3	9.79	19.8	5.54 cm (C)	***RhtMrkD1*** *–BS00036421*
ENPP	4A	*qENPP4A*	60.6	22.0–84.0	2.58	11.2	0.087 (C)	***dupw4*** *–BS99999979*
GY	2B	*qGY2B*	200	117–224	3.76	15.2	0.222 (C)	***BS00070104*** *–BS00009736*
	2D	*qGY2D*	53.0	42.0–63.0	4.94	20.7	0.236 t ha^{-1} (C)	***gwm132*** *–BS00022730*

Note. QTL, quantitative trait loci; PVE, phenotypic variation explained; SS, stem strength; SMS, stem material strength; SIL, stem internode length; SID, stem internode diameter; IWW, stem internode wall width; RPS, root plate spread; SRD, structural rooting depth; PH, plant height; ENPP, ear number per plant; GY, grain yield; Chr, chromosome; CI, confidence interval (LOD ±1.5); LOD, logarithm of odds (LOD threshold to declare significant QTL at a range of 2.94–3.13 resulted from a 1,000 permutation test at threshold of $\alpha = .10$ tail of the null distribution, except for *qENPP4A* where $\alpha = .15$ was considered); PVE, phenotypic variation explained.

[a]Additive effect with (C) indicates that the positive alleles come from parent Cadenza, and (A) indicates that positive alleles come from Avalon.

[b]Closest marker to the QTL is in bold.

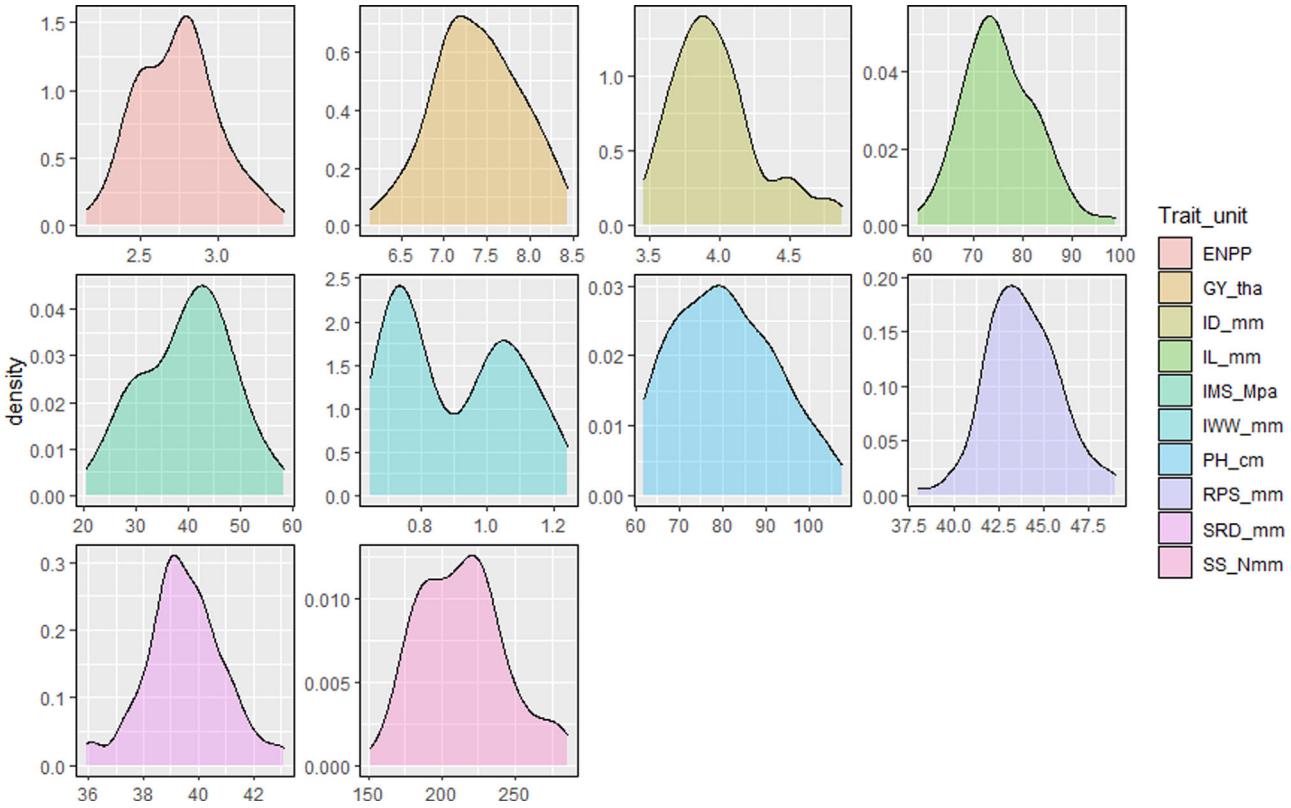

FIGURE 2 Smoothed frequency distributions (density plots) of grain yield (GY) and lodging traits (SS, stem strength; IMS, internode material strength; ID, internode diameter; IWW, internode wall width; IL, internode length; RPS, root plate spread; SRD, structural rooting depth; ENPP, ear number per plant; and PH, plant height). Data used to estimate density were combined adjusted means for genotypes across experiments

strength and internode material strength did not show significant interactions (data not shown).

3.5 | Anchorage strength characters

For anchorage strength characters QTL analysis detected only two genomic regions explaining 31.0 and 16.0% of the total PVE for RPS and SRD, respectively. Genomic regions located at 192 cM in chromosome 5B (closest marker *BS00070507*) and 154 cM in chromosome 6B (closest marker *wPt-4858*) showed a large positive effect on RPS (*qRPS5B*) and SRD (*qSRD6B*), respectively, given by the Cadenza allele (Table 2 and Figure 6).

3.6 | Leverage characters and grain yield

For leverage characters QTL models explained 62.5 and 11.2% of the total PVE for PH and ENPP, respectively. Three genomic regions located at 36.0 cM in chromosome 2D (*qPH2D*, closest marker *gwm261*), 145 cM in chromosome 3A (*qPH3A*, closest marker *wPt-9215*), and 61 cM in chromosome 4D (*qPH4D*, closest marker *RhtMrkD1*) had most of the additive effect (with positive alleles from Cadenza) on PH (PVE = 21.7, 16.1, and 23.3%, respectively). Genomic region located at 60.6 cM in chromosome 4A (closest marker *dupw4*) indicated positive effect given by Cadenza allele on ENPP (PVE = 11.2%, *qENPP4A*). For grain yield the QTL model explained 35.9% of the total PVE and identified two genomic regions located at 200 cM on chromosome 2B (*qGY2B*, closest marker *BS00070104*) and at 53.0 cM on chromosome 2D (*qGY2D*, closest marker *gwm132*) with significant additive effect from the Cadenza allele.

4 | DISCUSSION

Standard current methods for assessing lodging in wheat described in the literature (Berry et al., 2000; Berry et al., 2003c) require time-consuming sampling and measuring of stems and roots (Berry et al., 2003a). The absence of rapid phenotypic screening methodologies to assess lodging resistance demonstrates the necessity to explore and develop rapid and reliable methods with enough precision for breeding programs to improve lodging resistance in wheat. This study attempts to understand better the genetic control of key lodging traits and assess the possibility of developing

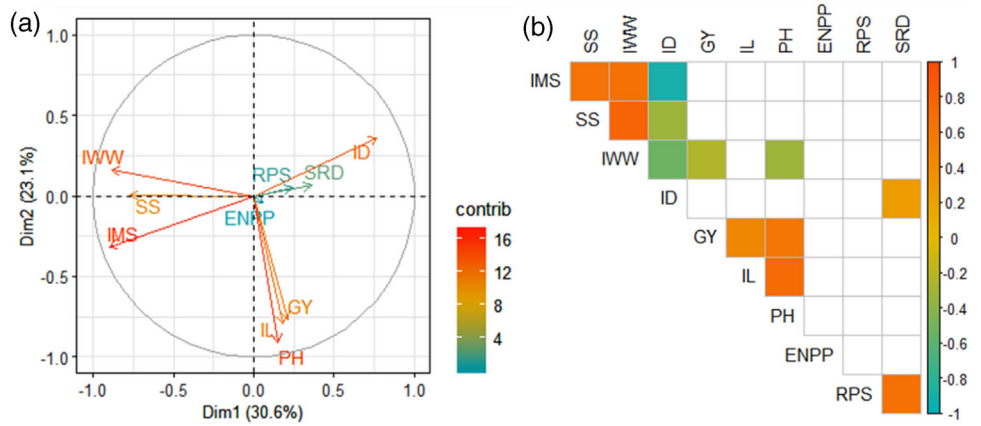

FIGURE 3 (a) Biplot of the interrelationships between grain yield (GY) and lodging traits (SS, stem strength; IMS, internode material strength; ID, internode diameter; IWW, internode wall width; IL, internode length; RPS, root plate spread; SRD, structural rooting depth; ENPP, ear number per plant; and PH, plant height). Percentage of variability explained by each dimension (Dim) is indicated in brackets and the contribution of each variable to this variability is indicated in the right colored scale (contrib). (b) Correlogram indicating significant Pearson correlations ($P < .05$) (not significant correlations in blank) between GY and lodging traits

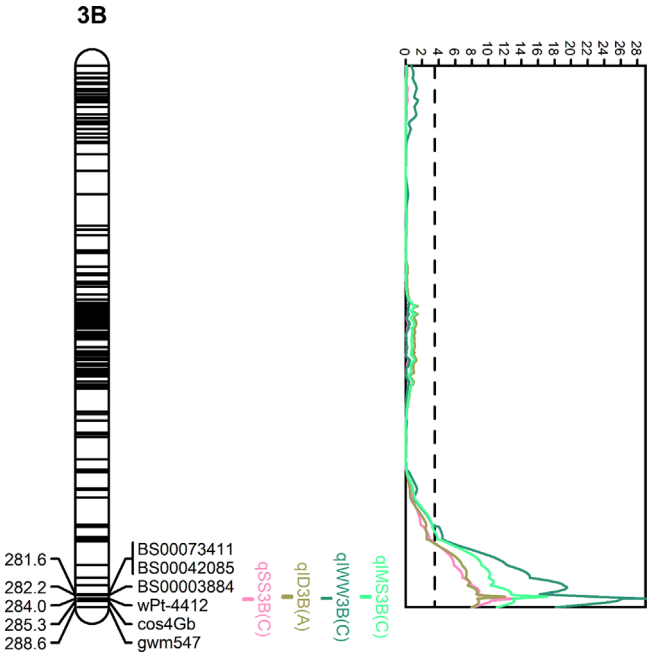

FIGURE 4 Major QTL region identified for stem strength characters: stem strength (pink), internode diameter (brown), internode wall width (green), and internode material strength (teal). Data are adjusted cross-experiment means for 84 lines of the Avalon × Cadenza doubled haploid population growing at High Mowthorpe and Sutton Bonington. (C) indicates that the positive alleles come from parent Cadenza, and (A) indicates that positive alleles come from Avalon

reliable genetic markers for them. In order to achieve this goal, key lodging traits have been targeted to develop a phenotypic database for the Avalon × Cadenza DH population in a 2-yr experiment in the UK. Together with this phenotypic database, genetic information in the public domain (http:www.cerealsdb.uk.net) has been used to implement QTL mapping tools that enabled the identification of a set of QTL with important genetic effects on stem strength characters, anchorage strength characters, leverage characters, and grain yield.

Genetic variation was observed for all the lodging traits and grain yield in this study. Similar results were observed in winter wheat (Berry et al., 2003b, 2007; Berry & Berry, 2015) and spring wheat (Piñera-Chavez et al., 2016b) for these lodging traits. Those authors also described significant G × E interactions that can reduce heritability across environments. Heritability values for lodging traits in the range of .73–.98 have been reported in winter wheat (Berry et al., 2007) and in the range of .11–.96 in spring wheat (Piñera-Chavez et al., 2016b). Lower values have also been found in winter wheat ranging from .17 to .90 (Berry, & Berry, 2015). Heritability values found in this study for the Avalon × Cadenza population ranged from .15 to .95. Anchorage strength characters showed the lowest heritability values in most of the aforementioned studies ranging from .11 to .40 (Berry & Berry, 2015; Piñera-Chavez et al., 2016b); averaging the heritability values across all these studies gives mean heritability values of above .60 for stem strength and .30 for root plate spread. These two traits have the greatest effects on strengthening the stem base and anchorage system and it is clear that an important percentage of the phenotypic variation is due to genetic effects. According to the QTL model, stem strength total PVE was estimated at 49.6%, which is most of the heritability observed in the cross-year analysis ($H^2 = .64$) that is explained by positive additive effect given by Cadenza allele on QTL *qSS1D* (*cfd19*) and *qSS3B* (*wPt-4412*). Interestingly, no epistasis was detected for those two QTL, which indicates their additive effects are independent of each other. For root plate spread

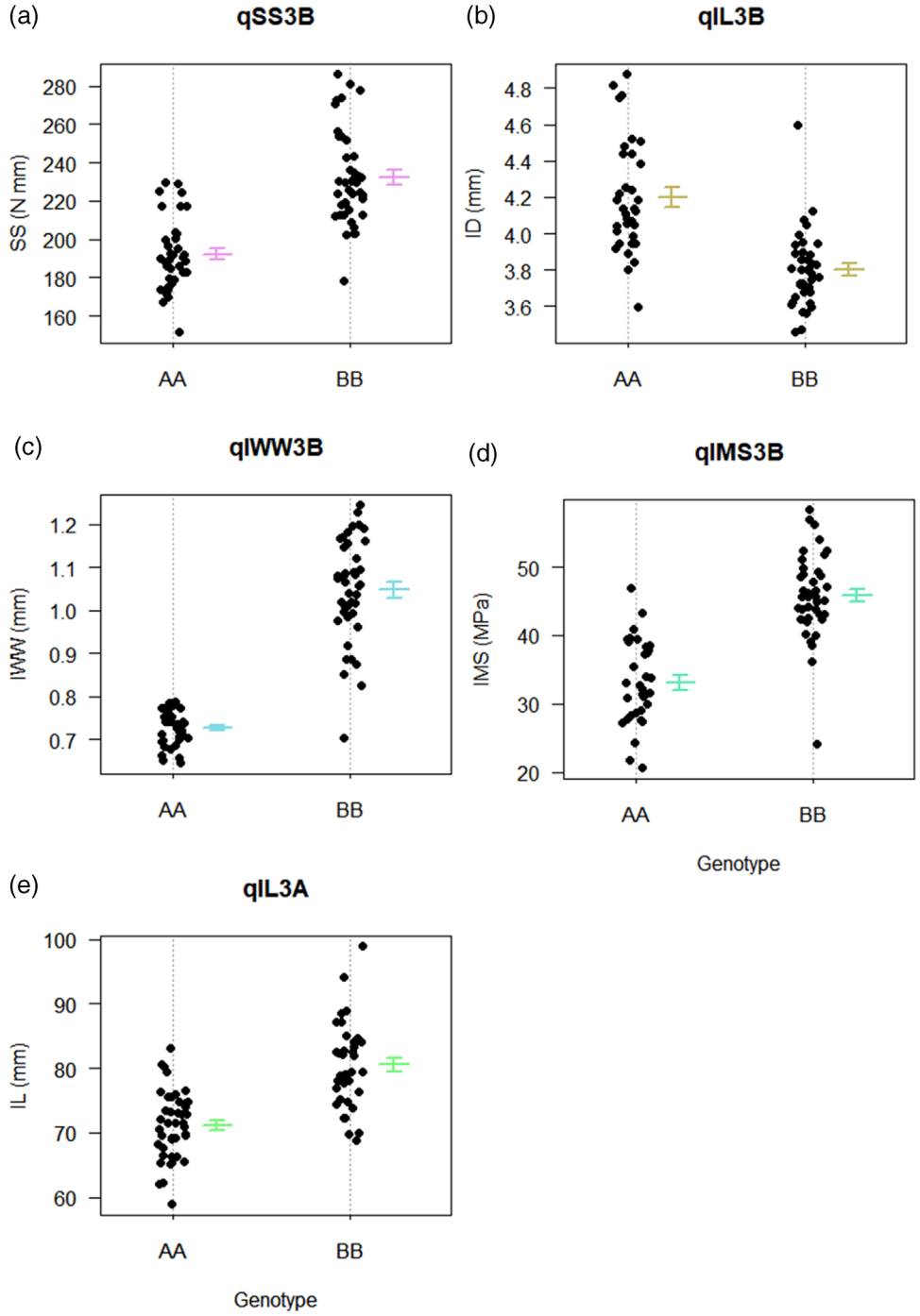

FIGURE 5 Effect of genotypes (at peak markers) Avalon (AA) and Cadenza (BB) on cross-year phenotypic means for (a) stem strength (SS); (b) internode diameter (ID), internode wall width (IWW), and internode material strength (IMS) at genomic region located at 283–284 cM (markers *BS00003884* and *wPt-4412*, respectively) in chromosome 3B (QTL *qSS3B*, *qqID3B*, *qIWW3B*, and *qIMS3B*, respectively), and internode length (IL) at linked QTL *qIL3A* (marker *bArc19*). Confidence intervals for the averaged phenotypic mean for each genotype with error bars at ±1 SE

total PVE explained by the QTL identified was 22.4%, which accounted for more than two-thirds of the cross-year heritability (H^2 = .33). Reduced plant height has a large effect on decreasing plant leverage (decreased lodging risk) (Berry et al., 2004) and is a highly heritable trait (values above .90 are normally reported). Thus, focusing on stem strength, root plate spread, and plant height can be an important strategy to improve lodging resistance. However, plant height has to be optimized carefully because high yields might not be compatible with reduction of plant height under 70 cm (Allan, 1986; Kertesz et al., 1991; Richards, 1992; Balyan & Singh, 1994; Miralles & Slafer, 1995; Flintham et al., 1997; Berry et al., 2015). Flintham et al. (1997) indicated that extreme dwarfism can reduce overall biomass which would counteract

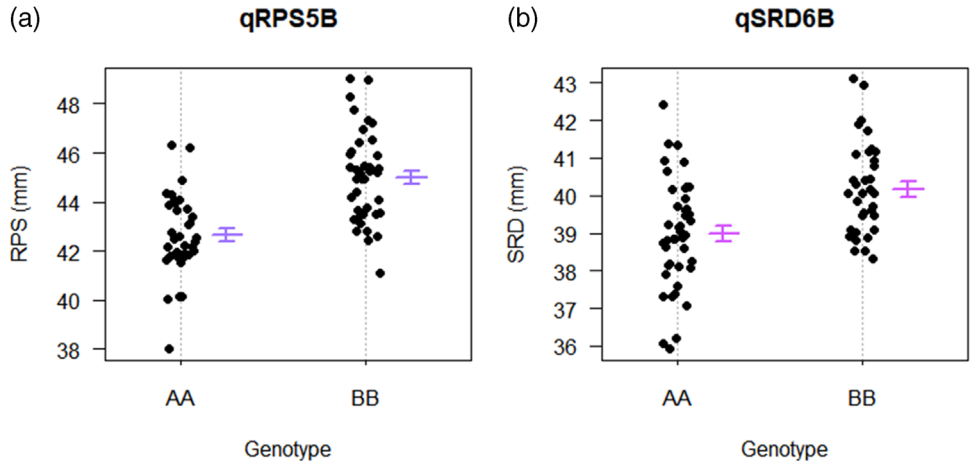

FIGURE 6 Effect of genotypes (at peak markers) Avalon (AA) and Cadenza (BB) on cross-year phenotypic means for (a) root plate spread (RPS) and (b) structural rooting depth (SRD) at linked QTL *qRPS5B* (*BS00070507*) and *qSRD6B* (*wPt-4858*), respectively. Confidence intervals for the averaged phenotypic mean for each genotype with error bars at ±1 SE

improvements in grain yield based on biomass (Reynolds et al., 2011). Moreover, recently introduced wheat varieties have been associated with no change in crop height (Berry et al., 2015) or even an increase of crop height (Aisawi et al., 2015) driven by selection bias or crop height genes linked to other traits or with pleiotropic effects (Law et al., 1978; Berry & Berry, 2015).

Inter-relationships among lodging traits identified by this and previous studies have not indicated a significant barrier to combining lodging-proof dimensions in a single wheat genotype (Figure 3, Berry et al., 2003b, 2007; Berry, & Berry, 2015; Piñera-Chavez et al., 2016b). However, for the Avalon × Cadenza DH population, negative correlations have been observed between internode diameter and the other components of stem strength. Berry et al. (2007) stated that the ideal strategy to increase stem strength in winter wheat would be to increase internode diameter and material strength (maintaining a minimum internode wall width) while investing the minimum amount of biomass. However, for spring wheat a very strong linkage (r = .84) between stem strength and internode wall width has been found that will be difficult to break, which may indicate that more than one option to combine trait dimensions has to be employed to strengthen the stem base (Piñera-Chavez et al., 2016b). This strong linkage (r = .78) between stem strength and internode wall width has also been found for the Avalon × Cadenza DH population. The negative correlation between stem strength and internode diameter is unusual and not aligned with the findings reported by the aforementioned studies and might be driven by the strong negative correlation (r = −.53) and the opposite direction of allelic effects that internode diameter (negative effect coming from Cadenza allele) had with the other stem strength components (positive effect coming from Cadenza allele). Solid stems typically observed for parent Cadenza may be related to this allelic effect that was previously reported for stem solidness in the Avalon × Cadenza DH population (Ma et al., 2015). This inconsistency may indicate that focusing on stem strength per se would be best.

A common genomic region affecting stem strength, internode material strength, internode diameter and internode wall width distributed in the interval 278–287 cM of chromosome 3B (Table 2) may indicate a gene that has pleiotropic effects on the overall SS and its components or tightly linked genes in this QTL region. The huge phenotypic variation explained by this QTL region for stem strength traits (e.g., overall stem strength) indicates that genetic effects of chromosome 3B alone can substantially increase lodging resistance. The pleiotropic effect or tight genetic linkage identified for this 3B region might also include a small effect on PH (*qPH3B*).

Impacts of reducing plant height from 103 cm to the theoretical optimum of 70 cm without increasing stem strength (214 N mm, mean stem strength observed in the Avalon × Cadenza) indicated that stem lodging probability per year can decrease from .73 to .08, respectively, for a crop yielding 8.9 t ha^{-1} (current grain yield in the UK according to DEFRA, 2019). Increasing stem strength by 28 N mm (QTL model additive effect) of a crop 130 cm tall yielding 8.9 t ha^{-1} will reduce its stem lodging probability from .73 to .59 (Figure 7a). This reduction effect would be equivalent to reduce 12 cm in the crop height.

As stated earlier, increasing stem strength with the minimum investment in biomass should be achieved by increasing internode material strength or internode diameter rather than internode wall width. Thus, stem strengthening from the 3B QTL is likely to lead to greater investment in stem biomass due to thicker stem walls. In some situations, this may cause a negative trade-off with grain yield resulting from the

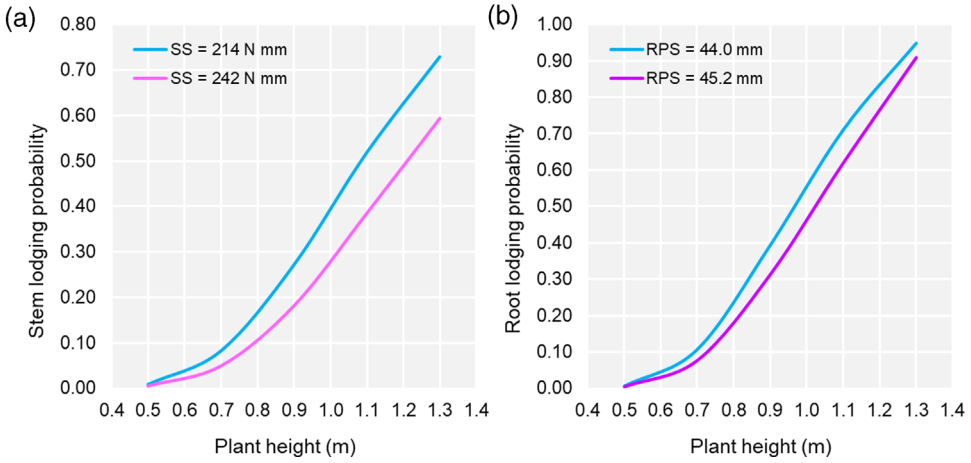

FIGURE 7 Stem strength (a) and root lodging (b) probability plotted against plant height using the mean stem strength and root plate spread observed (blue) and the mean stem strength and root plate spread plus the additive effect (**pink**) of stem strength QTL *qSS2D* and *qSS3B* (additive effect = 28 N mm) and root *QTL qRPS5B* (additive effect = 1.2 mm), respectively. Probability estimates are considering the other lodging model inputs from Berry et al. (2007) and a crop yielding 8.9 t ha^{-1} (average crop yield from the UK for 2019 according to DEFRA) established at 200 plants m^{-2} and 500 shoots m^{-2}

overlapping of yield-determining processes (Slafer & Rawson, 1994) and mechanical strength formation (Crook et al., 1994) before flowering, although this was not detected in this study. Nonetheless, developing a reliable marker in the interval located at 278–287 cM on chromosome 3B with positive effect from the Cadenza allele (*qSS3B, qIMS3B*, and *qIWW3B*) and at 51–60 cM on chromosome 2D with positive effect from the Avalon allele (*qID2D*) could be a criterion for designing a target genotype with stronger stems that can counteract trade-offs. The region at chromosome 3B also offers the advantage of a decreasing effect from Cadenza allele on plant height, which in turn can reduce lodging risk and stem biomass. Polygenic control of plant height identified for the Avalon × Cadenza population is in agreement with previous studies (Griffiths et al., 2012; Ma et al., 2015). This can help to optimize plant height independently of target stem characters.

A major finding of this study has also been the identification of QTL affecting RPS in the linkage Group 5B. Root plate spread has been described as the target anchorage strength trait to increase root lodging resistance (Berry et al., 2007). Impacts of reducing plant height from 130 cm to the theoretical optimum of 70 cm without increasing root plate spread (44 mm, mean root plate spread observed in the Avalon × Cadenza) indicated that root lodging probability per year can decrease from .94 to .04, respectively, for a crop yielding 8.9 t ha^{-1}. Increasing root plate spread by 1.2 mm (QTL model additive effect) of a crop 130 cm tall yielding 8.9 t ha^{-1} will reduce its root lodging probability from .95 to .91 (Figure 7b). This reduction effect would be equivalent to reduce 8 cm in the crop height.

In recent decades, QTL with effects on the strength, diameter, wall width, and material strength of the stem and the root plate spread and structural rooting depth of the crown root system indicating that increased lodging resistance in wheat can be accelerated by the implementation of molecular tools (Berry & Berry, 2015; Cook et al., 2004; Hai et al., 2005; Ma et al., 2015; Oiestad et al., 2017; Verma et al., 2005). In fact, QTL affecting stem strength, internode wall width, and internode diameter can be found on chromosomes 6A and 3B (Al-Qaudhy et al., 1988) and higher expression of gene *TaCM* (located at the distal region of chromosome 3BL) has already been linked to lodging resistance in wheat (Ma, 2009). A summary of the most recent studies and linkage groups or chromosomes where QTL regions affecting lodging characters is presented in Table 3. Quantitative trait loci with effects on stem strength and internode diameter were found on chromosome 3B for Avalon × Cadenza in the UK in this study and are comparable with QTL affecting stem strength and stem diameter of CA9613 × H1488 DH population located in the same chromosome under Northeast China growing conditions (Hai et al., 2005; Hai, 2006). Interestingly, markers *gwm285* and *gwm547* delimiting the section 134.9–288.5 cM of chromosome 3B (containing *qSS3B* and *qID3B*) for Avalon × Cadenza also delimited a section of chromosome 3B where a QTL related to stem strength and diameter of CA9613 × H1488 was found. Microsatellite markers *gwm247*, *gwm340*, and *gwm547* linked to a QTL explaining around 76% of PVE located on chromosome 3BL have been related to stem solidness (Cook et al., 2004). This has a similar location to the QTL *qIWW3B* affecting internode wall width of Avalon × Cadenza, which was very close to marker *gwm547*. The QTL affecting root plate spread were identified on chromosome 5B for Avalon × Cadenza in this study and Solstice × Xi19 in the UK (Berry et al., 2008; Berry & Berry, 2015). All chromosomes with QTL affecting plant height identified for Avalon ×

TABLE 3 Review of recent studies with identified loci regions affecting lodging-related traits in wheat. Chromosome or linkage group where the QTL is located is given

Source	Env.	Map type	Map length	Germplasm	SS	IMS	IL	ID	IWW	RPS	SRD	PH
Present study	UK	SNP, SSR, DArT	4,686	Avalon × Cadenza	1D, 3B	2D, 3B	1A, 3A	2D, 3B, 4B	3B, 4B, 4D	5B	6B	2D, 3A, 3B,4D
Berry and Berry (2015)	UK	SSR, DarT	2,466	Savannah × Rialto	6A	3A	–	3A, 4D	3A, 7D	7D	7A, 7D	1D, 2A, 3A, 6A, 7D
Berry and Berry (2015)	UK	SSR, DarT	2,503	Solstice × Xi19	1A, 6A	3A	–	4D	3A, 6A, 6B	5B	–	3A, 4A, 6A
(Verma et al., 2005)	UK	SSR	2,959	Milan × Catbird	2D[a]	–	4B	–	1B	–	2D	4B, 4D
Hai et al. (2005)	China	SSR	2,308	CA9613 × H1488	3A, 3B	–	–	3B	2D	–	–	–
Atkinson et al. (2015)	Controlled (phytotron)	SNP	–	Savannah × Rialto	–	–	–	–	–	6D	6D, 7D	–
Cook et. al. (2004)	USA	SSR	–	Rampart × Jerry	–	–	–	–	3BL	–	–	–
(Oiestad et al., 2017)	USA	SNP	–	Near isogenic lines	–	–	–	–	3BL	–	–	–
Griffiths et al. (2012)[b]	UK	SSR, DArT	–	Charger × Bagder, Spark × Rialto, Savannah × Rialto, Avalon × Cadenza	–	–	–	–	–	–	–	1A, 1B, 1D, 2A, 2B, 2D. 3A, 3B, 4B, 4D, 5A, 5B, 6A, 6B, 6D

Note. QTL, quantitative trait loci; SS, stem strength; IMS, stem material strength; IL, stem internode length; ID, stem internode diameter; IWW, stem internode wall width; RPS, root plate spread; SRD, structural rooting depth; PH, plant height; DArTs, diversity arrays technology.

[a]Breaking strength.

[b]Meta-QTLs from four populations.

Cadenza in this study can be matched with the chromosomes for plant height meta-QTL from four doubled-haploid populations reported by Griffiths et al. (2012). Peak markers or markers within the confidence intervals (*gwm261*, *wPt-9215*, *wPt-4412*, and *RhtMrkD1*) and allelic effects can also be matched with these meta-QTL.

In order to describe in more detail key findings, the sequence of markers closest to QTL *qSS3B* (*wPt-4412*) and *qRPS5B* (*BS00070507*) were subjected to the reference wheat genome sequence Ensembl Plants *Triticum aestivum* version 101.4 (IWGSC) (Yates et al., 2020). Marker closest to *qSS3B* was located at the physical position 826,153,965–826,154,263 bp and was very close to the gene TraesCS3B02G607725 (826,127,602–826,128,868 bp, transcript length of 1,267 bps) coding for protein P-loop NTPase (P-loop containing nucleoside triphosphate hydrolase) domain superfamily. P-loop NTPases are protein domains related to most biochemical and mechanical processes in the cell (Aravind et al., 2004). The marker closest to *qRPS5B* was located at the physical position 437,622,993–437,623,103 bp and was very close to the gene TraesCS5B02G255000 (437,572,048–437,573,082 bp, transcript length of 1,035 bps) coding for protein kinase-like domain superfamily. Plant protein kinases have been related to diurnal and circadian regulation, cell cycle regulation, developmental processes, and so forth (Lehti-Shiu, & Shiu, 2012). In soybean [*Glycine max* (L.) Merr.], a root-specific WNK (lysine deficient protein kinase 1) kinase homolog (*GmWNK1*) showed regulation effects on root system architecture in response to abscisic acid (ABA) and osmotic signals (Wang et al., 2010). Recently, Cui et al. (2018) reported that a heat CBL-interacting protein kinase (*CIPK23*) enhanced root system development through longer roots and higher number of lateral roots.

In conclusion, this study describes the genetic variation and associations of the lodging-related traits targeted for improving lodging resistance in wheat. Significant genetic variation was identified for the Avalon × Cadenza DH

population, although G × E interactions were also found. Stem strength traits were highly heritable, whereas root or anchorage strength traits had low heritability. Inter-relationships between traits have implications for achieving a lodging-resistant ideotype with the minimum investment of biomass. This was inferred from the negative correlation between internode diameter with stem strength, and the strong positive correlation between stem strength and internode wall width, both of which increase stem biomass required per unit of stem strength. However, possible strategies have emerged from the QTL mapping of this DH population to counteract these implications. In general, QTL for stem strength on chromosome 3B and internode diameter on chromosome 2D could help to identify a stem lodging resistant ideotype with a minimum investment of biomass and QTL for root plate spread on chromosome 5B for an increased root lodging resistant ideotype. More importantly, these QTL on chromosomes 3B and 5B were shown to be consistent among different genetic backgrounds, potentially making them more reliable for breeding purposes.

Based on this study and previous investigations with plant materials with different genetic backgrounds, it appears that regions of chromosomes 3B and 6A have major effects on stem strength. Future prospects will include the validation and/or fine mapping of QTL on chromosomes 3B (overall stem strength), 2D (internode diameter), and 5B (root plate spread) affecting key lodging-resistant traits of Avalon × Cadenza to find reliable validated markers that could be used in marker assisted selection (MAS) or genomic selection (GS) for root and stem lodging resistance.

ACKNOWLEDGMENTS

The authors acknowledge the funding and support given by CIMMYT and the Secretaria de Agricultura y Desarrollo Rural (SADER) through the Cultivos para Mexico Initiative (before MasAgro Initiative), CONACYT (Consejo Nacional de Ciencia y Tecnologia) for providing a postgraduate scholarship (no. 214700), and the Beachell-Borlaug International Scholars Program for providing a complementary research fellowship to Francisco J. Piñera-Chavez. We are also grateful to the University of Nottingham-Crop Science and ADAS High Mowthorpe staff for their support.

AUTHOR CONTRIBUTIONS

Francisco J. Piñera-Chavez: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Writing-original draft; Writing-review & editing. Peter M. Berry: Conceptualization; Funding acquisition; Investigation; Methodology; Supervision; Writing-review & editing. Michael J. Foulkes: Conceptualization; Funding acquisition; Project administration; Supervision; Writing-review & editing. Sivakumar Sukumaran: Writing-review & editing. Matthew P. Reynolds: Conceptualization; Funding acquisition; Supervision; Writing-review & editing.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

ORCID

Francisco J. Piñera-Chavez https://orcid.org/0000-0001-7868-2396
Michael J. Foulkes https://orcid.org/0000-0002-7765-8340
Sivakumar Sukumaran https://orcid.org/0000-0003-4088-4624
Matthew P. Reynolds https://orcid.org/0000-0002-4291-4316

REFERENCES

Aisawi, K. A. B., Reynolds, M. P., Singh, R. P., & Foulkes, M. J. (2015). The physiological basis of the genetic progress in yield potential of CIMMYT spring wheat cultivars from 1966 to 2009. *Crop Science*, *55*, 1749–1764. https://doi.org/10.2135/cropsci2014.09.0601

Al-Qaudhy, W., Morris, R., Mumm, R. F., & Hanna, M. A. (1988). Chromosomal locations of genes for traits with lodging in winter wheat. *Crop Science*, *28*, 631–635. https://doi.org/10.2135/cropsci1988.0011183X002800040012x

Allan, R. E. (1986). Agronomic comparisons among wheat lines nearly isogenic for three reduced-height genes. *Crop Science*, *26*, 707–710. https://doi.org/10.2135/cropsci1986.0011183X002600040014x

Aravind, L., Iyer, L. M., Leipe, D. D., & Koonin, E. V. (2004). A novel family of P-loop NTPases with an unusual phyletic distribution and transmembrane segments inserted within the NTPase domain. *Genome Biology*, *5*. https://doi.org/10.1186/gb-2004-5-5-r30

Atkinson, J. A., Wingen, L. U., Griffiths, M., Pound, M. P., Gaju, O., Foulkes, M. J., Le Gouis, J., Griffiths, S., Bennett, M. J., King, J., & Wells, D. M. (2015). Phenotyping pipeline reveals major seedling root growth QTL in hexaploid wheat. *Journal of Experimental Botany*. https://doi.org/10.1093/jxb/erv006

Bai, C., Liang, Y., & Hawkesford, M. J. (2013). Identification of QTLs associated with seedling root traits and their correlation with plant height in wheat. *Journal of Experimental Botany*, *64*, 1745–1753. https://doi.org/10.1093/jxb/ert041

Balyan, H. S., & Singh, O. (1994). Pleiotropic effects of GA-insensitive Rht genes on grain yield and its component characters in wheat. *Cereal Research Communications*, *22*, 195–200.

Berry, P. M., & Berry, S. T. (2015). Understanding the genetic control of lodging-associated plant characters in winter wheat (*Triticum aestivum* L.). *Euphytica*. https://doi.org/10.1007/s10681-015-1387-2

Berry, P. M., Berry, S. T., & Spink, J. H. (2008). Identification of genetic markers for lodging resistance in wheat. HGCA Research Project Report 441. Home Grown Cereals Authority.

Berry, P. M., Griffin, J. M., Sylvester-Bradley, R., Scotta, R. K., Spink, J. H., Baker, C. J. & Clare, R. W. (2000). Controlling plant form through husbandry to minimise lodging in wheat. *Field Crops Research*, *67*, 59–81. https://doi.org/10.1016/S0378-4290(00)00084-8

Berry, P. M., Kendall, S., Rutterford, Z., Orford, S., & Griffiths, S. (2015). Historical analysis of the effects of breeding on the height of winter wheat (*Triticum aestivum*) and conse-

quences for lodging. *Euphytica*, *203*, 375–383. https://doi.org/10.1007/s10681-014-1286-y

Berry, P. M., Spink, J., Sterling, M., & Pickett, A. A. (2003a). Methods for rapidly measuring the lodging resistance of wheat cultivars. *Journal of Agronomy and Crop Science*, *189*, 390–401. https://doi.org/10.1046/j.0931-2250.2003.00062.x

Berry, P. M., Spink, J. H., Gay, A. P., & Craigon, J. (2003b). A comparison of root and stem lodging risks among winter wheat cultivars. *Journal of Agricultural Science*, *141*, 191–202. https://doi.org/10.1017/S002185960300354X

Berry, P. M., Sterling, M., Baker, C. J., Spink, J., & Sparkes, D. L. (2003c). A calibrated model of wheat lodging compared with field measurements. *Agriculture and Forest Meteorology*, *119*, 167–180. https://doi.org/10.1016/S0168-1923(03)00139-4

Berry, P. M., Sterling, M., Spink, J. H., Baker, C. J., Sylvester-Bradley, R., Mooney, S. J., Tams, A. R., & Ennos, A. R. (2004). Understanding and reducing lodging in cereals. *Advances in Agronomy*, *84*, 217–271. https://doi.org/10.1016/S0065-2113(04)84005-7

Berry, P. M., Sylvester-Bradley, R., & Berry, S. (2007). Ideotype design for lodging-resistant wheat. *Euphytica*, *154*, 165–179. https://doi.org/10.1007/s10681-006-9284-3

Broman, K. W., Wu, H., Sen, Ś., & Churchill, G. A. (2003). R/qtl: QTL mapping in experimental crosses. *Bioinformatics*, *19*, 889–890. https://doi.org/10.1093/bioinformatics/btg112

Churchill, G. A., & Doerge, R. W. (1994). Empirical threshold values for quantitative trait. *Genetics*, *138*, 963–971 https://doi.org/10.1093/genetics/138.3.963

Conway, G. (1997). *The Doubly Green Revolution. Food for all in the 21st century*. Penguin Group.

Cook, J. P., Wichman, D. M., Martin, J. M., Bruckner, P. L., & Talbert, L. E. (2004). Identification of microsatellite markers associated with a stem solidness locus in wheat. *Crop Science*, *44*, 1397–1402. https://doi.org/10.2135/cropsci2004.1397

Crespo-Herrera, L. A., Crossa, J., Huerta-Espino, J., Autrique, E., Mondal, S., Velu, G., Vargas, M., Braun, H. J., & Singh, R. P. (2017). Genetic yield gains in CIMMYT's international Elite Spring Wheat Yield Trials by modeling the genotype × environment interaction. *Crop Science*, *56*, 1–13. https://doi.org/10.2135/cropsci2016.06.0553

Crook, M. J., Ennos, A. R., & Sellers, E. K. (1994). Structural development of the shoot and root systems of two winter wheat cultivars, *Triticum aestivum* L. *Journal of Experimental Botany*, *45*, 857–863. https://doi.org/10.1093/jxb/45.6.857

Cui, X. Y., Du, Y. T., Fu, J. D., Yu, T.-F., Wang, C.-T., Chen, M., Chen, J., Ma, Y.-Z., & Xu, Z.-S. (2018). Wheat CBL-interacting protein kinase 23 positively regulates drought stress and ABA responses. *BMC Plant Biology*, *18*, 93. https://doi.org/10.1186/s12870-018-1306-5

DEFRA (2019). *Farming statistics. Final crop areas, yields, livestock populations and agricultural workforce*. http://www.statistics.gov.uk/hub/index.html

Fischer, T., Byerlee, D., & Edmeades, G. (2014). Crop yields and global food security. *Australian Centre for International Agricultural Research*, *660*.

Flintham, J. E., Borner, A., Worland, A. J., & Gale, M. D. (1997). Optimizing wheat grain yield: Effects of Rht (gibberellin-insensitive) dwarfing genes. *Journal of Agricultural Science*, *128*, 11–25. https://doi.org/10.1017/S0021859696003942

Foulkes, M. J., Reynolds, M. P., & Sylvester-Bradley, R. (2009). Genetic improvement of grain crops: Yield potential. In V. Sadras & D. Calderini (Eds.), *Crop physiology*. (pp. 355–385). Academic Press. https://doi.org/10.1016/B978-0-12-374431-9.00015-3

Gerard, G. S., Crespo-Herrera, L. A., Crossa, J., Mondal, S., Velu, G., Juliana, P., Huerta-Espino, J., Vargas, M., Rhandawa, M. S., Bhavani, S., Braun, H., & Singh, R. P. (2020). Grain yield genetic gains and changes in physiological related traits for CIMMYT's High Rainfall Wheat Screening Nursery tested across international environments. *Field Crops Research*, *249*, 107742. https://doi.org/10.1016/j.fcr.2020.107742

Griffiths, S., Simmonds, J., Leverington, M., Wang, Y., Fish, L., Sayers, L., Alibert, L., Orford, S., Wingen, L., & Snape, J. (2012). Meta-QTL analysis of the genetic control of crop height in elite European winter wheat germplasm. *Theoretical and Applied Genetics*, *29*, 159–171. https://doi.org/10.1007/s11032-010-6534-x

Hai, L. (2006). Analysis of genetic diversity among current spring wheat varieties and breeding for improved yield stability of wheat (*Triticum aestivum* L.). [Doctoral dissertation, Justus-Liebig-University Giessen].

Hai, L., Guo, H., Xiao, S., Jiang, G., Zhang, X., Yan, C., Xin, Z., & Jia, J. (2005). Quantitative trait loci (QTL) of stem strength and related traits in a doubled-haploid population of wheat (*Triticum aestivum* L.). *Euphytica*, *141*, 1–9. https://doi.org/10.1007/s10681-005-4713-2

Kelbert, A. J., Spaner, D., Briggs, K. G., & King, J. R. (2004). The association of culm anatomy with lodging susceptibility in modern spring wheat genotypes. *Euphytica*, *136*, 211–221. https://doi.org/10.1023/B:EUPH.0000030668.62653.0d

Keller, M., Karutz, C., Schmid, J. E., Stamp, P., Winzeler, M., Keller, B., & Messmer, M. M. (1999). Quantitative trait loci for lodging resistance in a segregating wheat × spelt population. *Theoretical and Applied Genetics*, *98*, 1171–1182. https://doi.org/10.1007/s001220051182

Kertesz, Z., Flintham, J. E., & Gale, M. D. (1991). Effects of Rht dwarfing genes on wheat grain yield and its components under eastern European conditions. *Cereal Research Communications*, *19*, 297–304.

Knott, S. A., & Haley, C. S. (1992). A simple regression method for mapping quantitative trait loci in line crosses using flanking markers. *Heredity*, *69*, 315–324. https://doi.org/10.1038/hdy.1992.131

Lander, E. S., & Botstein, S. (1989). Mapping mendelian factors underlying quantitative traits using RFLP linkage maps. *Genetics*, *121*, 185. https://doi.org/10.1093/genetics/121.1.185.

Law, C. N., Snape, J. W., & Worland, A. J. (1978). The genetical relationship between height and yield in wheat. *Heredity*, *40*, 133–151. https://doi.org/10.1038/hdy.1978.13

Lehti-Shiu, M. D., & Shiu, S. H. (2012). Diversity, classification and function of the plant protein kinase superfamily. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 2619–2639. https://doi.org/10.1098/rstb.2012.0003

Li, Z. K., Jiang, X. L., Peng, T., Shi, C. L., Han, S. X., Tian, B., Zhu, Z. L., & Tian, J. C. (2014). Mapping quantitative trait loci with additive effects and additive × additive epistatic interactions for biomass yield, grain yield, and straw yield using a doubled haploid population of wheat (*Triticum aestivum* L.). *Genetics and Molecular Research*, *13*, 1412–1424. https://doi.org/10.4238/2014.February.28.14

Lopes, M. S., Reynolds, M. P., Manes, Y., Singh, R. P., Crossa, J., & Braun, H. J. (2012). Genetic yield gains and changes in associated traits of CIMMYT spring bread wheat in a "Historic" set representing 30 years of breeding. *Crop Science*, *52*, 1123–1131. https://doi.org/10.2135/cropsci2011.09.0467

Ma, J., Wingen, L. U., Orford, S., Fenwick, P., Wang, J., & Griffiths, S. (2015). Using the UK reference population Avalon × Cadenza as a platform to compare breeding strategies in elite Western European bread wheat. *Molecular Breeding*, *35*, 70. https://doi.org/10.1007/s11032-015-0268-7

Ma, Q.-H. (2009). The expression of caffeic acid 3-O-methyltransferase in two wheat genotypes differing in lodging resistance. *Journal of Experimental Botany*, *60*, 2763–2771. https://doi.org/10.1093/jxb/erp132

Miralles, D. J., & Slafer, G. A. (1995). Yield, biomass and yield components in dwarf, semi-dwarf and tall isogenic lines of spring wheat under recommended and late sowing dates. *Plant Breeding*, *114*, 392–396. https://doi.org/10.1111/j.1439-0523.1995.tb00818.x

Niu, L., Feng, S., Ru, Z., Li, G., Zhang, Z., & Wang, Z. (2012). Rapid determination of single-stalk and population lodging resistance strengths and an assessment of the stem lodging wind speeds for winter wheat. *Field Crops Research*, *139*, 1–8. https://doi.org/10.1016/j.fcr.2012.10.014

Oiestad, A. J., Martin, J. M., Cook, J., Varella, A. C., & Giroux, M. J. (2017). Identification of candidate genes responsible for stem pith production using expression analysis in solid-stemmed wheat. *The Plant Genome*, *10*. https://doi.org/10.3835/plantgenome2017.02.0008

Piñera-Chavez, F. J., Berry, P. M., Foulkes, M. J., Jesson, M. A., & Reynolds, M. P. (2016a). Avoiding lodging in irrigated spring wheat. I. Stem and root structural requirements. *Field Crops Research*, *196*, 325–336. https://doi.org/10.1016/j.fcr.2016.06.009

Piñera-Chavez, F. J., Berry, P. M., Foulkes, M. J., Molero, G., & Reynolds, M. P. (2020). Optimizing phenotyping methods to evaluate lodging risk for wheat. *Field Crops Research*, *258*, 107933. https://doi.org/10.1016/j.fcr.2020.107933

Piñera-Chavez, F. J., Berry, P. M., Foulkes, M. J., Molero, G., & Reynolds, M. P. (2016b). Avoiding lodging in irrigated spring wheat. II. Genetic variation of stem and root structural properties. *Field Crops Research*, *196*, 64–74. https://doi.org/10.1016/j.fcr.2016.06.007

Reynolds, M., Bonnett, D., Chapman, S. C., Furbank, R. T., Manès, Y., Mather, D. E., & Parry, M. A. J. (2011). Raising yield potential of wheat. I. Overview of a consortium approach and breeding strategies. *Journal of Experimental Botany*, *62*, 439–52. https://doi.org/10.1093/jxb/erq311

Ribaut, J.-M., de Vicente, M. C., & Delannay, X. (2010). Molecular breeding in developing countries: Challenges and perspectives. *Current Opinion in Plant Biology*, *13*, 213–218. https://doi.org/10.1016/j.pbi.2009.12.011

Richards, R. A. (1992). The effect of dwarfing genes in spring wheat in dry environments. I. Agronomic characteristics. *The Australian Journal of Agricultural Research*, *43*, 517–527. https://doi.org/10.1071/AR9920517

SAS Institute Inc. (2004). *SAS System for Windows. Version 9.1*. SAS Institute, Inc.

Sen, S., & Churchill, G. A. (2001). A statistical framework for quantitative trait mapping. *Genetics*, *159*, 371–387.

Slafer, G. A., & Rawson, H. M. (1994). Sensitivity of wheat phasic development to major environmental factors: A re-examination of some assumptions made by physiologists and modellers. *Australian Journal of Plant Physiology*, *21*, 393. https://doi.org/10.1071/PP9940393

Snape, J. W., Foulkes, M. J., Simmonds, J., Leverington, M., Fish, L. J., Wang, Y., & Ciavarrella, M. (2007). Dissecting gene × environmental effects on wheat yields via QTL and physiological analysis. *Euphytica*, *154*, 401–408. https://doi.org/10.1007/s10681-006-9208-2

Tadesse, W., Sanchez-Garcia, M., & Assefa, S. G. (2019). Genetic gains in wheat breeding and its role in feeding the world. *Crop Breeding, Genetics and Genomics*, 1–28. https://doi.org/10.20900/cbgg20190005

Tripathi, S. C., Sayre, K. D., Kaul, J. N., & Narang, R. S. (2003). Growth and morphology of spring wheat (*Triticum aestivum* L.) culms and their association with lodging: Effects of genotypes, N levels and ethephon. *Field Crops Research*, *84*, 271–290. https://doi.org/10.1016/S0378-4290(03)00095-9

Van Ooijen, J. W. (2011). JoinMap® 4.1, Software for the calculation of genetic linkage maps in experimental populations. Kyazma B.V.

Verma, V., Foulkes, M. J., Worland, A. J., Sylvester-Bradley, R., Caligari, P. D. S., & Snape, J. W. (2004). Mapping quantitative trait loci for flag leaf senescence as a yield determinant in winter wheat under optimal and drought-stressed environments. *Euphytica*, *135*, 255–263. https://doi.org/10.1023/B:EUPH.0000013255.31618.14

Verma, V., Worland, A. J., Sayers, E. J., Fish, L., Caligari, P. D. S., & Snape, J. W. (2005). Identification and characterization of quantitative trait loci related to lodging resistance and associated traits in bread wheat. *Plant Breeding*, *124*, 234–241. https://doi.org/10.1111/j.1439-0523.2005.01070.x

Wang, Y., Suo, H., Zheng, Y., Liu, K., Zhuang, C., Kahle, K. T., Ma, H., & Yan, X. (2010). The soybean root-specific protein kinase GmWNK1 regulates stress-responsive ABA signaling on the root system architecture. *Plant Journal*, *64*, 230–242. https://doi.org/10.1111/j.1365-313X.2010.04320.x

Wiersma, J. J., Dai, J., & Durgan, B. R. (2011). Optimum timing and rate of trinexapac-ethyl to reduce lodging in spring wheat. *Agronomy Journal*, *103*, 864–870. https://doi.org/10.2134/agronj2010.0398

Yang, M., Ding, G., Shi, L., Feng, J., Xu, F., & Meng, J. (2010). Quantitative trait loci for root morphology in response to low phosphorus stress in *Brassica napus*. *Theoretical and Applied Genetics*, *121*, 181–193. https://doi.org/10.1007/s00122-010-1301-1

Yates, A. D., Achuthan, P., Akanni, W., Allen, J., Allen, J., Alvarez-Jarreta, J., Amode, M. R., Armean, I. M., Azov, A. G., Bennett, R., Bhai, J., Billis, K., Boddu, S., Carlos Marugán, J., Cummins, C., Davidson, C., Dodiya, K., Fatima, R., Gall, A., … Flicek, P. (2020). *Nucleic Acids Research*, *48*, D682–D688. https://doi.org/10.1093/nar/gkz966

Zadoks, J. C., Chang, T. T., & Konzak, C. F. (1974). A decimal code for the growth stages of cereals. *Weed Research*, *14*, 415–421 https://doi.org/10.1111/j.1365-3180.1974.tb01084.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Piñera-Chavez FJ, Berry PM, Foulkes MJ, Sukumaran S, Reynolds MP. Identifying quantitative trait loci for lodging-associated traits in the wheat doubled-haploid population Avalon × Cadenza. *Crop Science*. 2021;*61:* 2371–2386. https://doi.org/10.1002/csc2.20485